ECOLOGICAL MORPHOLOGY OF FRESHWATER STREAM FISHES

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ABSTRACT

Variation and interrelations of 56 morphological features were studied in 44 species of stream-living fishes. The morphological characters are interpreted ecologically based on information in the literature, character correlations, factor analysis, gut content analyses, and field observations.

The results show extensive significant linear correlations among many of the characters. A number of multiple associations were identified and ranked in the factor analysis. The ecological meanings of these latter results are that the major morphological trends in these fishes are: (1) differentiation in feeding strategy between "lie-in-wait" biting predators and cruising suction feeders; (2) habitat separation according to water velocity; (3) vertical habitat separation; and (4) feeding differentiation between small insectivores and large omnivores.

Gut content data were also examined by factor analysis. The results showed that for these freshwater stream fishes, size of prey is the most important component in separating the diets of different species and vertical position of the prey is the second most important component. Various correlations between the size and location of the prey and several morphological characteristics are also discussed.

How much about the biological roles of a species is determinable from its anatomical features and what particular functions are regularly associated with which features? These twin questions are at the heart of much current work in the areas of functional and ecological morphology (Bock and von Wahlert, 1965; Hespenheide, 1973). The purpose of the research presented here is to provide some answers to these questions for certain North Carolina freshwater stream fishes.

The relationship between the form of fishes and their life habits has been the subject of casual writings from at least the time of the ancient Hindus (Hora, 1935). More recently, Hubbs (1941) provided a good generalized background on this topic, and subsequent works by Alexander (1967), Aleev (1969), and Gosline (1971) provide modern and comprehensive summaries of various aspects.

In this paper I (1) summarize earlier theoretical and experimental studies in the literature relevant to probable functional interpretation of various morphological features of fishes and (2) present the results of my own research using correlation analysis, factor analysis, and gut content analysis on these same morphological features. Additional discussion of the structure of stream fish communities based on this morphological assessment of ecological roles is presented elsewhere (Gatz, 1979).

MATERIALS AND METHODS

Fishes and Streams.—Seines of various lengths were used to collect fishes at six stations in each of three streams in the Piedmont of North Carolina. The streams sampled were East Prong Little Yadkin (Stokes County, Pee Dee drainage), Mud Creek (Durham County, Cape Fear drainage), and Maho Creek (Person County, Roanoke drainage). Collections were made at all seasons over a two year

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*Present Address: Department of Zoology, Ohio Wesleyan University, Delaware, Ohio 43015 period (August, 1972, through August, 1974). All species thus collected were included in the analysis of morphology.

Samples of ten adult individuals were measured for each of the 33 species for which I had collected sufficient material. These species were *Esox americanus*, the redfin pickerel, *Esox niger*, the chain pickerel, *Clinostomus funduloides*, the rosyside dace, *Hybopsis hypsinotus*, the highback chub, *Nocomis leptocephalus*, the bluehead chub, *Notemigonus crysoleucas*, the golden shiner, *Notropis alborus*, the whitemouth shiner, *Notropis altipinnis*, the highfin shiner, *Notropis analostanus*, the satinfin shiner, *Notropis ardens*, the rosefin shiner, *Notropis cerasinus*, the crescent shiner, *Notropis chiliticus*, the redlip shiner, *Notropis procne*, the swallowtail shiner, *Phoxinus oreas*, the mountain redbelly dace, *Semotilus atromaculatus*, the creek chub, *Castostomus commersoni*, the white sucker, *Erimyzon oblongus*, the creek chubsucker, *Ictalurus nebulosus*, the brown bullhead, *Noturus insignis*, the margined madtom, *Aphredoderus sayanus*, the pirate perch, *Gambusia affinis*, the mosquitofish, *Centrarchus macropterus*, the flier, *Lepomis auritus*, the redbreast sunfish, *Lepomis cyanellus*, the green sunfish, *Lepomis gibbosus*, the pumpkinseed, *Lepomis gulosus*, the warmouth, *Lepomis macrochirus*, the bluegill, *Micropterus salmoides*, the largemouth bass, *Pomoxis nigromaculatus*, the black crappie, *Etheostoma flabellare*, the fantail darter, *Etheostoma fusiforme*, the swamp darter, *Etheostoma olmstedi*, the tessellated darter, and *Perca flavescens*, the yellow perch. For the 11 rarer species, all individuals collected were used. These 11 species were *Anguilla rostrata*, the American eel, *Umbra pygmaea*, the eastern mudminnow, *Notropis hudsonius*, the spottail shiner, *Moxostoma anisurum*, the silver redhorse, *Moxostoma erythrurum*, the golden redhorse, *Moxostoma pappillosum*, the suckermouth redhorse, *Moxostoma robustum*, the smallfin redhorse, *Ictalurus catus*, the white catfish, *Ictalurus punctatus*, the channel catfish, *Enneacanthus gloriosus*, the bluespotted sunfish, and *Percina crassa*, the Piedmont darter. The conclusions drawn concerning the interpretation of the morphological features should not, however, be generalized to groups of fishes with grossly different structure or habitats.

Morphological Characteristics.

— Fifty-six morphological characteristics were chosen for study. Determinations of 50 of these characters were made on each individual fish. In addition, six characters related to superficial brain morphology were measured on a single individual of each species. A preliminary study of the brains of several individuals of a single species (*Notropis altipinnis*) had indicated very low variance in these characters.

Each of the 56 characters is listed below along with the method of determination. All length measurements less than 120 mm were made with vernier calipers to the nearest 0.1 mm and length measurements longer than this were made with a millimeter rule. All area measurements were made from outline drawings using a planimeter. For all qualitative characters, the various manifestations or states of the characteristic were coded numerically using integers. These character state codes for qualitative characters are indicated in parentheses below where relevant.

Superficial body and body shape characters

1. Standard length in this study is the straight line distance from the most anterior part of the head to the terminus of the vertebral column.

2. Pigmentation pattern was visually classified into one of four qualitative categories: (1) silvery or reflective sides; (2) countershading with a dark lateral band; (3) mottled pattern or vertical bars; and (4) countershading without either silveriness or a lateral band.

3. Completeness of the lateral line canal was recorded as being complete (2), incomplete (1), or lacking (0).

4. Position of the lateral line canal was recorded as lacking (0), curving dorsally (1), horizontal (2), or curving ventrally (3).

5. Relative head length was measured as the straight line distance from the most anterior point on the upper lip to the posterior margin of the opercular membrane divided by the standard length. In large adult *Lepomis auritus*, the redbreast sunfish, excessive hypertrophy of the opercular membrane occurs. For this species the posterior limit for the head length measurement was taken at a point where a subjectively "reasonable" opercular membrane might end.

6. Flatness index is the maximum body depth divided by the maximum body width.

7. Relative body depth is the maximum body depth divided by the standard length.

8. Index of trunk shape is the perpendicular distance from the anterior tip of the head to an imaginary vertical line at the point of maximum body depth divided by the standard length.

9. Relative peduncle length is the horizontal distance from a vertical line at the level of the posterior margin of the base of the most posterior median fin to the terminus of the vertebral column divided by the standard length.

10. Caudal peduncle flatness index is the depth of the peduncle at its midpoint divided by the width at the same point.

Caudal fin characters

11. Aspect ratio of the caudal fin may be calculated as span squared divided by area (Nursall, 1958; Ovchinnikov, 1971). Span or maximum vertical distance and area were measured from an outline drawing of a maximally extended caudal fin.

12. Caudal span / body depth ratio is the span of the caudal fin divided by the maximum body depth.

13. Number of caudal fin rays is the total count of all rays reaching further than one half the distance from the base of the caudal fin to its distal edge. For fishes in the families Cyprinidae, Catostomidae and Centrarchidae, this count is the same as the count for caudal rays given by Hubbs and Lagler (1958), i.e., this count is the number of branched rays plus two (principal ray count). For fishes in other families such as Esocidae and Ictaluridae, some "rudimentary rays" (Hubbs and Lagler, 1958) were also counted. The number of "rudimentary rays" counted was determined by the length criterion set in this study. In the case of *Anguilla*, in which the rays of the dorsal, anal and caudal fins all form a continuous series, this character was not used.

Paired fin characters

14. Pectoral fin length is the distance from the base of the pectoral fin to the extreme tip of the fin at its longest point divided by the standard length of the fish.

15. Aspect ratio of the pectoral fin is estimated as a length to width ratio.

16. Relative pectoral fin area is the surface area of the pectoral fin divided by the surface area of the fish. Outline drawings of one pectoral fin and of the entire fish in lateral view were made by tracing around the objects. Relative pectoral fin area was taken to be the ratio of the areas of these two drawings.

17. Relative distance of the pectoral fin from the center of gravity of the fish was measured from the medial base of the pectoral fin to the point of center of gravity (CG) on the lateral surface of the fish and divided by standard length. This point CG was determined by balancing the fish on the tip of a dissecting needle. Notice that this distance can be small both when the fin is slightly anterior to the CG or posterior to the CG and thus is a different character than #19 below.

18. Pectoral fin shape was coded based on a subjective evaluation of whether the fins were (1) rounded, (2) intermediate, or (3) pointed.

19. Position of the pectoral fin relative to the center of gravity is an assignment of how the pectoral fin when adpressed against the lateral surface of the body relates to a transverse plane through the

point CG as defined above. Four possible relationships were recognized: (1) fin wholly anterior to the plane; (2) fin originating anterior to CG and extending posterior to the plane; (3) fin originating at the level of the CG plane; and (4) fin originating posterior to the CG.

20. Number of pectoral fin rays were counted on alizarin stained fins. All rays (including spines), no matter what length, were counted.

21. Pelvic fin length was measured in a manner strictly analogous to pectoral fin length (#14, above).

22. Aspect ratio of the pelvic fin was estimated as a length to width ratio.

23. Relative pelvic fin area was measured analogously to relative pectoral fin area (#16, above).

24. Relative distance of the pelvic fin from the center of gravity of the fish was measured analogously to the similar character, number 17, for the pectoral fin.

25. Pelvic fin shape was categorized similarly to pectoral fin shape.

26. Position of the pelvic fin relative to the center of gravity was an assignment using the same four character states as were used in the analogous character for the pectoral fin (#19, above).

27. Number of pelvic fin rays was counted like the number of pectoral fin rays.

28. Position of the dorsal fin relative to the center of gravity was an assignment using the same four character states as were used in the analogous character for the pectoral fin (#19, above). Assignment was made according to the position of the entire dorsal fin base relative to the CG plane.

Head characters

29. Relative eye size was the diameter of the eye between fleshy orbits along an anterior-posterior axis divided by the standard length.

30. Position of the eyes involved assigning character states depending upon whether the eyes were placed laterally on the head (1), or were oriented dorsolaterally either slightly (2) or greatly (3).

31. Eye pigmentation was a categorization according to the presence or absence and orientation of any dark bands of pigmentation running across the cheek and through the eye. Possible categories and their character state codes were: (0) no such pigment; (1) horizontal line through the eye; (2) vertical line through the eye; and (3) both horizontal and vertical lines through the eye.

32. Position of the mouth was coded according to the position of the opening of the mouth when closed. Character states were (1) supraterminal if the lower jaw extended anterior to the upper, (2) terminal if the jaws were subequal, (3) subterminal if the lower jaw ended slightly posterior to the upper, (4) inferior if the opening was clearly recessed from the anterior edge of the head, and (5) ventral if the mouth was positioned along the ventral surface of the body.

33. Orientation of the mouth was coded according to the orientation of an imaginary plane perpendicular to the longitudinal axis of the body and tangential to both lips of the open mouth. Character states were: (1) dorsal if the plane faced above the vertical, (2) anterior if the plane was vertical, (3) oblique if the plane faced obliquely downward, and (4) ventral if the plane was horizontal.

34. Relative width of the mouth was the interior lateral dimension of the opening when the mouth was fully opened, divided by the standard length of the fish.

35. Relative height of the mouth was the interior dorso-ventral dimension of the opening when the mouth was fully opened, divided by the standard length of the fish.

36. Index of protrusion was measured as the ratio of snout length with the mouth open to snout length with the mouth closed where snout length is the distance from the interior surface of the anterior edge of the bony orbit of the eye to the anterior margin of the upper jaw at its midpoint.

37. Number of barbels was the count of these sensory structures about the mouth.

38. Number of branchiostegal rays was a count of these structures which support the gill coverings. Alizarin staining was used to facilitate counting.

39. Presence of jaw teeth was coded (0) if none were present, (1) if teeth were on the mandible and premaxillary and/or maxillary only, and (2) if teeth were on both jaws and additional bones of the roof of the mouth such as the palatine or vomer.

40. Shape of jaw teeth was coded (0) if such teeth were absent, (1) if all teeth were small sharp points, and (2) if both small pointed and larger canine teeth were present.

41. Hypertrophy of teeth on the pharyngeal arches was coded (0) if all teeth on the fifth pharyngeal arch were small, and (1) if the teeth were hypertrophied.

42. Shape of the pharyngeal teeth was coded (1) if all teeth were short pointed structures, (2) if the teeth were hooked, (3) if the teeth had cutting edges, and (4) if the teeth had flattened grinding surfaces.

43. Number of gill rakers was a count of the total number of rakers which were visible after staining with alizarin on both ascending and descending limbs of the lateral surface of the first arch.

44. Shape of the middle gill raker was measured as the length divided by the width of that raker. In the case of pickerels, genus *Esox*, in which the gill rakers are represented by flat plates only, the length was taken to be zero and hence the value for this character was also zero.

45. Finer structure of the gill rakers was coded (0) if each raker was smooth, (1) if each raker had a ridged surface, (2) if each raker had fewer than 50 fine sharp teeth on it, and (3) if each raker had more than 50 fine teeth on it.

Internal body characters

46. Relative volume of the swim bladder was estimated by dividing the volume of the swim bladder by the volume of the fish. The latter volume was determined by measuring displacement volume. Swim bladder volume was measured in different ways in different families of fishes. In fishes such as cyprinids and catostomids in which the swim bladder could be removed intact, it was and then filled with water using a syringe and its displacement volume determined. In fishes which have swim bladders with rather rigid walls and definite median partitions such as centrarchids and ictalurids, the lateral portion of the left side of the bladder was removed and the volume of water required to fill the right half determined. Swim bladder volume was estimated to be twice this volume. For fishes like esocids which have thin walled, non-removeable swim bladders, the volume was estimated mathematically using the formula for the volume of a cylinder. The estimate of radius used was obtained from measurements of both lateral and dorso-ventral diameters of the swim bladder in a series of transverse sections of the entire fish.

47. Relative length of the swim bladder was the ratio of the length of the swim bladder to the standard length of the fish.

48. Relative gut length was measured as the length of the entire alimentary canal posterior to the pharynx divided by the standard length. The digestive tract was dissected from the fish and mesenteries and was then stretched slightly to straighten bends when the measurement was taken.

49. Number of pyloric caeca was a count of the caeca at the junction of the stomach and the intestine.

50. Percentage of red muscle in the caudal peduncle was estimated as a percentage of total muscle in transverse sections made near the middle of the peduncle. Sections were made using a freezing microtome, stained for fats (which are higher in concentration in red muscle than in white), and mounted on slides. Planimeter estimates of the areas of the red and white muscle were made on drawings of the slides traced from the image projected by a microprojector.

Brain characters

51. Relative size of the forebrain was determined by measurement of the length and the width of both forebrain lobes and

expressing the average of these two dimensions as a proportion of the same two measurements of the optic lobes. Brains were exposed dorsally, and thus this character was an estimate of the amount of the dorsal surface of the brain which was occupied by the forebrain relative to the amount occupied by the optic lobes.

52. Relative size of the optic lobes was determined by expressing the average of the length and width of these lobes as a proportion of the total length of the brain from the anterior end of the forebrain to the posterior end of the vagal lobes.

53. Relative size of the cerebellum is, as are all further brain characters, analogous to the character on the forebrain (#51, above) in that the average of the length and width of the lobe(s) under consideration is expressed in relation to the average of the length and width of the optic lobes.

54. Relative size of the vagal lobes, as indicated above, compares the dimensions of the vagal and optic lobes.

55. Relative size of the facial lobes compares the size of these lobes to the optic lobes.

56. Relative size of the acoustic tubercles compares the size of these lobes to the optic lobes.

Gut Content Analysis.—As an aid to the interpretation of the morphological characteristics, gut contents were examined throughout the entire length of the digestive tract of all individuals that were studied morphologically. Replacements were substituted for all fishes which had either completely empty tracts or tracts with wholly digested material. Each replacement was selected to be of as nearly as possible the same size and the same date of collection as the original fish.

Items found in the gut were identified as completely as possible. Grouped categories of food items were used in the final analysis of foods taken. These categories were: (1) fishes, (2) copepods, (3) ostracods, (4) aquatic insects, (5) terrestrial insects, (6) crayfishes, (7) isopods and amphipods, (8) diatoms, (9) filamentous algae, (10) molluscs, (11) non-insect terrestrial invertebrates, and (12) vascular plants. Size of food items (greatest linear dimension) was measured directly from intact items and was estimated from the dimensions of an identified part in the case of broken or digested organisms. The presence of sand and silt in the gut was recorded also.

Gut content data were coded to facilitate numerical treatment. Following in the tradition of fishery biology (Lagler, 1956), two ways of considering prey were recognized: number of items of a given category, and percentage volume of all food belonging to a given category. These two types of information were incorporated into the gut content characters by forming two characters for each of the 12 previously listed categories of food items. Frequency characters were given character state codes according to the scheme: (1) never taken, (2) present in up to 20% of tracts , (3) 21-40%, (4) 41-60%, (5) 61-80%, and (6) 81-100%. Percentage volumetric importance character state values were based on the percentage of digestive tracts examined in which item(s) of the given category formed a subjectively determined largest percentage volume of food of a single type, i.e., primary food. Character state values for these characters were: (1) not taken at all, (2) taken, but never the primary food category, (3) sometimes the primary food category, (4) taken more often as the primary food than items in any other category, but still not in the majority of individuals of the species, (5) primary food category in the majority of individuals, and (6) the only food utilized. The importance character and frequency character can be identical for any given category. This was the case for categories 7, 10, and 12 above, and in these cases I used only a single character representing both frequency and importance in subsequent analyses.

The prey size data were coded as two characters: absolute prey size and relative prey size. For both, the coded value for each species was derived from an estimated overall mean size of an item of prey. Character states for the absolute prey size character were: (1) ≤ 2 mm, (2) 5 mm, (3) 10 mm, (4) 20 mm, (5) 40 mm, and (6) ≥60 mm. For the relative prey size character, the estimated average absolute prey size was divided by the average standard length for the species sample to give a proportion. This was coded according to the scheme: (1) ≤ 0.05, (2) 0.10, (3) 0.15, (4) 0.20, (5) 0.25, and (6) ≥0.30.

Mathematical Methods

Simple linear correlations.—Two types of correlation coefficient were determined between the species means of all characters for all 33 common species. Pearson product-moment correlation coefficients were calculated using the Biomedical Computer Program BMD P1M. Spearman rank-order correlation coefficients were calculated with procedure Spearman of the Statistical Analysis System, North Carolina State University. The model underlying the former type requires that the two variables being correlated each exhibit a normal distribution. This was not the case for a number of the characters in this study; therefore, the latter type coefficient was also calculated because the model for it does not require that the variables fit any particular distribution.

The Bonferonni technique was used in assigning significance to the correlation coefficients. This is a very conservative procedure which allows one to know the probability of making a family Type I error. A Type I error is made if a hypothesis is rejected when it is true (in this case, the recognition of correlations as significant which are not). All statistical tests which employ the same set of observations belong to the same family. Thus, in the correlation analysis described here, the 55 correlations of each morphological character with every other character is a family of tests because the same set of observations is used 55 times. In order for the probability of making a Type I error to equal $P < 0.05$ in an entire family of tests, the Bonferonni technique requires that each individual test be conducted at a probability of 0.05 / n where n is the number of tests in the family. For the present study, 0.05 / 55 is approximately equal to 0.001. Therefore, Pearson correlation coefficients were considered to be significant if they were greater than or equal to 0.546 ($df = 31$, $P < 0.001$) and Spearman correlation coefficients, if they were greater than or equal to 0.571 ($df = 31$, $P < 0.001$). This technique controls Type I errors because hypotheses of no relationship between two variables are rejected only at a very small value of P, i.e., when correlations are quite likely significant. Of course, the probability of making a Type II error (failure to reject a hypothesis when it is false, i.e., in this case, failure to recognize a significant correlation) is, as always, inversely related to the probability of making a Type I error.

Factor Analysis.—Factor analysis is a multivariate statistical technique that generates a small number of hypothetical factors which reproduce the linear correlations between variables in the original data set. Each factor so generated is a linear combination of covarying portions of the original variables. Interpretation of the hypothetical factors is facilitated by orthogonal rotation using the varimax criterion. Orthogonal rotation of the factors makes each factor statistically independent; i.e., the factors are not correlated. The varimax criterion maximizes the variance of each factor by causing as many factor loadings (i.e., coefficients relating the original variables to factors) as possible to tend toward zero or one. Thus each of the originally measured variables tends to make either a large or a negligible contribution to each of the hypothetical factors. The chief value of factor analysis is as an aid in the recognition of overall trends in the variation and covariation of a large number of variables. Additionally, because factor analysis also indicates the proportion of the total pattern of variation accounted for by each factor, it is of value in understanding the relative strength of trends in variation.

Factor analysis was performed in this study using Biomedical Computer Program BMD O8M. Orthogonal rotation using the varimax criterion was used. In accordance with the suggestion of Harman (1967), only factors with eigenvalues greater than one were considered. This prevents "overfactorization," i.e., the generation of hypothetical constructs that are explaining trends in error variances rather than in the pattern of variation in the original variables.

RESULTS AND DISCUSSION

In the first three sections below the results of the three major types of analyses are presented individually. Each analysis by itself provides some useful information in the understanding of fish morphology. In a fourth section, then, all these results are integrated with information from the literature in order to provide a functional, ecological interpretation of each of the morphological features studied.

Simple Linear Correlations.—Extensive correlations between characters were determined. Using the previously defined criterion for significance, 500 of the 3080 Pearson product-moment coefficients were significant as were 494 of the Spearman rank-order coefficients. However, 200 of these differed between types of coefficient. I tested whether part of the difference in result might have been due to differences in character distributions. The total set of characters was divided into two groups: those in which the values showed continuous variation (e.g., proportional measurements) and those in which the values were discrete (e.g., fin ray counts and qualitative characters with integer character state codes). Chi-square analysis was then used to test the null hypothesis that the two types of correlation coefficient acted at random with regard to these different types of characters. In both cases the hypothesis of randomness was rejected. Of correlations unique to the Spearman rank-order correlation coefficient, significantly more ($P < 0.005$) involved characters with discrete character state distributions than one should expect at random. Of correlations unique to the Pearson product-moment correlation coefficient, significantly more ($P < 0.05$) involved characters with continuous variation. However, visual examination of frequency plots of character state values indicated that characters with discrete character state distributions did not as a class necessarily show the greatest deviation from normal distributions. As a consequence of all this, I have somewhat arbitrarily listed below only the approximately 400 correlations determined to be significant by both types of coefficient. If the r in both cases was greater than 0.717 so that the coefficient of determination was greater than 50%, the correlation has been marked with an asterisk. Some of these many correlations are discussed individually below in the interpretation of morphological characters. Additional discussion of the methodological problem of which correlation coefficient is appropriate for use is found in Gatz (1975).

1. *Standard length* – Positive correlations: number of gill rakers. Negative correlations: *relative peduncle length; relative pectoral fin area.

2. *Pigmentation pattern* – No significant correlations.

3. *Completeness of lateral line* – Positive correlations: position of lateral line. No significant negative correlations.

4. *Position of lateral line* – Positive correlations: completeness of lateral line; aspect ratio of caudal fin; caudal span / body depth; number of caudal fin rays; position of pectoral fin; hypertrophy of pharyngeal teeth; percentage of red muscle. Negative correlations: pelvic fin aspect ratio; presence of jaw teeth; shape of jaw teeth; fine structure of gill rakers.

5. *Relative head length* – Positive correlations: *relative body depth; position of pectoral fin; position of pelvic fin; *width of mouth; *height of mouth; *presence of jaw teeth; *fine structure of gill rakers; number of pyloric caeca. Negative correlations: *caudal span / body

depth; *distance of pectoral fin from CG; position of dorsal fin; position of the mouth; hypertrophy of pharyngeal teeth.

6. *Flatness index* – Positive correlations: *relative body depth; *pelvic fin length, *relative eye size; protrusibility of the mouth. No significant negative correlations.

7. *Relative body depth* – Positive correlations: *relative head length; *flatness index; *pelvic fin length; *distance of pelvic fin from CG; relative eye size; protrusibility of the mouth. Negative correlations: *caudal span / body depth; distance of pectoral fin from CG.

8. *Index of trunk shape* – No significant correlations.

9. *Relative peduncle length* – No significant positive correlations. Negative correlations: *standard length; number of gill rakers.

10. *Caudal peduncle flatness index* – Positive correlations: relative size of forebrain. No significant negative correlations.

11. *Aspect ratio of caudal fin* – Positive correlations: position of lateral line; number of caudal fin rays; number of pectoral fin rays; position of pelvic fin; position of dorsal fin; hypertrophy of pharyngeal teeth; percentage of red muscle. Negative correlations: pelvic fin aspect ratio; position of jaw teeth.

12. *Caudal span / body depth* – Positive correlations: position of lateral line; number of caudal fin rays; distance of pectoral fin from CG; *position of pelvic fin, number of pelvic fin rays; *position of dorsal fin; *hypertrophy of pharyngeal teeth. Negative correlations: *relative head length; *relative body depth; pectoral fin length; position of pectoral fin; *pelvic fin length; *distance of pelvic fin from CG; *pelvic fin shape; *presence of jaw teeth; *fine structure of gill rakers.

13. *Number of caudal fin rays* – Positive correlations: position of lateral line; aspect ratio of caudal fin; caudal span / body depth; *position of pelvic fin; *number of pelvic fin rays; hypertrophy of pharyngeal teeth; percentage of red muscle. Negative correlations: position of pectoral fin; aspect ratio of pelvic fin; pelvic fin shape; relative size of optic lobes.

14. *Pectoral fin length* – Positive correlations: position of pectoral fin; *pelvic fin length; *distance of pelvic fin from CG; *pelvic fin shape; relative size of eye. Negative correlations: caudal span / body depth; pelvic fin position; *number of pelvic fin rays.

15. *Aspect ratio of the pectoral fin* – Positive correlations: pectoral fin shape. No significant negative correlations.

16. *Relative pectoral fin area* – No significant positive correlations. Negative correlations: standard length; *relative length of swim bladder.

17. *Distance of pectoral fin from center of gravity* – Positive correlations: caudal span / body depth; position of dorsal fin; hypertrophy of pharyngeal teeth. Negative correlations: *relative head length; *relative body depth; position of pectoral fin; *width of the mouth; presence of jaw teeth; number of pyloric caeca.

18. *Pectoral fin shape* – Positive correlations: pectoral fin aspect ratio. No significant negative correlations.

19. *Position of the pectoral fin* – Positive correlations: relative head length; caudal span / body depth; pectoral fin length; position of lateral line; pelvic fin length; pelvic fin aspect ratio; distance of pelvic fin from CG; pelvic fin shape; fine structure of gill rakers. Negative correlations: distance of pectoral fin from CG; number of caudal fin rays; *position of pelvic fin; *number of pelvic fin rays; percentage of red muscle.

20. *Number of pectoral fin rays* – Positive correlations: aspect ratio of caudal fin; position of the dorsal fin; hypertrophy of pharyngeal teeth. No significant negative correlations.

21. *Pelvic fin length* – Positive correlations: *flatness index; *relative body depth; *pectoral fin length; position of the pectoral fin; *distance of the pelvic fin from CG; pelvic fin shape; relative eye size; fine structure of gill rakers. Negative correlations: *caudal span / body depth;

position of the pelvic fin; number of pelvic fin rays; position of the dorsal fin.

22. *Aspect ratio of the pelvic fin* – Positive correlations: position of the pectoral fin; distance of pelvic fin from CG; pelvic fin shape; presence of jaw teeth; shape of jaw teeth; fine structure of gill rakers; *relative size of optic lobes. Negative correlations: position of the lateral line; aspect ratio of caudal fin; number of caudal fin rays; *position of pelvic fin; number of pelvic fin rays; hypertrophy of pharyngeal teeth; *percentage of red muscle; relative size of facial lobes.

23. *Relative pelvic fin area* – Positive correlations: shape of jaw teeth. No significant negative correlations.

24. *Distance of pelvic fin from center of gravity* – Positive correlations: relative head length; *relative body depth; *pectoral fin length; position of pectoral fin; *pelvic fin length, pelvic fin aspect ratio; *pelvic fin shape; *fine structure of gill rakers; number of pyloric caeca. Negative correlations: *caudal span / body depth; *position of pelvic fin; *number of pelvic fin rays; *position of dorsal fin.

25. *Pelvic fin shape* – Positive correlations: *pectoral fin length; position of pectoral fin; pelvic fin length; aspect ratio of pelvic fin; *distance of pelvic fin from CG; relative eye size; presence of jaw teeth; *fine structure of gill rakers; *relative size of optic lobes. Negative correlations; *caudal span / body depth; number of caudal fin rays; *number of pelvic fin rays: *position of pelvic fin; *position of dorsal fin; hypertrophy of pharyngeal teeth; percentage of red muscle; relative size of cerebellum; relative size of facial lobes.

26. *Position of pelvic fin* – Positive correlations: position of lateral line; aspect ratio of caudal fin; *caudal span / body depth; *number of pelvic fin rays; *position of dorsal fin; *hypertrophy of pharyngeal teeth; percentage of red muscle; relative size of facial lobes. Negative correlations: pectoral fin length; *position of pectoral fin; *aspect ratio of pelvic fin; *distance of pelvic fin from CG; *pelvic fin shape; presence of jaw teeth; shape of jaw teeth; relative size of optic lobes; pelvic fin length; *fine structure of gill rakers; number of pyloric caeca.

27. *Number of pelvic fin rays* – Positive correlations: caudal span / body depth; *number of caudal fin rays; *position of pelvic fin; position of dorsal fin; hypertrophy of pharyngeal teeth; relative size of facial lobes. Negative correlations: *pectoral fin length; *position of pectoral fin; pelvic fin length; aspect ratio of pelvic fin; *distance of pelvic fin from CG; *pelvic fin shape; relative eye size; presence of jaw teeth; fine structure of gill rakers; number of pyloric caeca; relative size of optic lobes.

28. *Position of dorsal fin* – Positive correlations: aspect ratio of caudal fin; caudal span / body depth; distance of pectoral fin from CG; number of pectoral fin rays; *position of pelvic fin; number of pelvic fin rays; *hypertrophy of pharyngeal teeth; percentage of red muscle. Negative correlations: relative head length; position of pectoral fin; pelvic fin length; *distance of pelvic fin from CG; *pelvic fin shape; *presence of jaw teeth; shape of jaw teeth; *fine structures of gill rakers; number of pyloric caeca.

29. *Relative eye size* – Positive correlations: *flatness index; relative body depth; pectoral fin length; pelvic fin length; protrusibility of the mouth. Negative correlations: number of pelvic fin rays; relative size of cerebellum.

30. *Position of the eyes* – No significant correlations.

31. *Eye pigmentation* – No significant positive correlations. Negative correlations: percentage of red muscle.

32. *Position of the mouth* – Positive correlations: *orientation of the mouth; *relative size of facial lobes. Negative correlations: relative head length; width of the mouth; *height of the mouth.

33. *Orientation of the mouth* – Positive correlations: *position of the mouth. Negative correlations: *height of the mouth.

34. *Relative width of the mouth* – Positive correlations: *relative head length;

*height of the mouth; presence of jaw teeth. Negative correlations: *distance of pectoral fin from CG; position of the mouth; hypertrophy of pharyngeal teeth.

35. *Relative height of the mouth* – Positive correlations: *relative head length; *width of the mouth. Negative correlations: *position of the mouth; orientation of the mouth.

36. *Protrusibility of the mouth* – Positive correlations: *flatness index; relative body depth; relative eye size; relative swim bladder volume. No significant negative correlations.

37. *Number of barbels* – Positive correlations: *relative size of forebrain; *relative size of cerebellum. No significant negative correlations.

38. *Number of branchiostegal rays* – Positive correlations: presence of jaw teeth; *shape of jaw teeth. Negative correlations: *hypertrophy of pharyngeal teeth; percentage of red muscle.

39. *Presence of jaw teeth* – Positive correlations: *relative head length; aspect ratio of pelvic fin; pelvic fin shape; width of the mouth; number of branchiostegal rays; *shape of jaw teeth; fine structure of gill rakers; number of pyloric caeca; relative size of optic lobes. Negative correlations: position of lateral line; *caudal span / body depth; distance of pectoral fin from CG; position of the pelvic fin; number of pelvic fin rays; *position of dorsal fin; *hypertrophy of pharyngeal teeth; percentage of red muscle.

40. *Shape of jaw teeth* – Positive correlations: relative head length; aspect ratio of pelvic fin relative pelvic fin area; *number of branchiostegal rays; *presence of jaw teeth; fine structure of gill rakers; relative size of optic lobes. Negative correlations: position of lateral line; aspect ratio of caudal fin; position of pelvic fin; position of dorsal fin; *hypertrophy of pharyngeal teeth; percentage of red muscle.

41. *Hypertrophy of pharyngeal teeth* – Positive correlations: position of lateral line; aspect ratio of caudal fin; *caudal span / body depth; number of caudal fin rays; distance of pectoral fin from CG; number of pectoral fin rays; *position of pelvic fin; number of pelvic fin rays; *position of dorasl fin; percentage of red muscle. Negative correlations: relative head length; aspect ratio of pelvic fin; pelvic fin shape; width of the mouth; *number of branchiostegal rays; *presence of jaw teeth; *shape of jaw teeth; fine structure of gill rakers; relative size of optic lobes.

42. *Shape of pharyngeal teeth* – No significant correlations.

43. *Number of gill rakers* – Positive correlations: standard length; fine structure of gill rakers. Negative correlations: relative peduncle length.

44. *Shape of gill rakers* – No significant correlations.

45. *Fine structure of gill rakers* – Positive correlations: relative head length; position of pectoral fin; distance of pelvic fin from CG; pelvic fin length; pelvic fin aspect ratio; pelvic fin shape; presence of jaw teeth; shape of jaw teeth; number of gill rakers; number of pyloric caeca; relative size of optic lobes. Negative correlations: position of lateral line; caudal span / body depth; position of pelvic fin; number of pelvic fin rays; position of dorsal fin; hypertrophy of pharyngeal teeth; percentage of red muscle; relative size of cerebellum; relative size of facial lobes.

46. *Relative volume of the swim bladder* – Positive correlations: *relative length of swim bladder. No significant negative correlations.

47. *Relative length of the swim bladder* – Positive correlations: *relative volume of swim bladder. Negative correlations: *relative pectoral fin area.

48. *Relative gut length* – No significant correlations.

49. *Number of pyloric caeca* – Positive correlations: relative head length; distance of pelvic fin from CG; presence of jaw teeth; fine structure of gill rakers. Negative correlations: distance of pectoral fin from CG; pelvic fin position; number of pelvic fin rays; position of dorsal fin.

50. *Percentage of red muscle in the peduncle* – Positive correlations: position

of lateral line; aspect ratio of caudal fin; number of caudal fin rays; position of pelvic fin; position of dorsal fin; hypertrophy of pharyngeal teeth. Negative correlations: position of pectoral fin; *aspect ratio of pelvic fin; pelvic fin shape; eye pigmentation; number of branchiostegal rays; presence of jaw teeth; shape of jaw teeth; fine structure of gill rakers; relative size of optic lobes.

51. *Relative size of the forebrain* — Positive correlations: caudal peduncle flatness index. No significant negative correlations.

52. *Relative size of the optic lobes* – Positive correlations: aspect ratio of pelvic fin; *pelvic fin shape; presence of jaw teeth; shape of jaw teeth; fine structure of gill rakers. Negative correlations: number of caudal fin rays; *position of pelvic fin; number of pelvic fin rays; hypertrophy of pharyngeal teeth; percentage of red muscle; relative size of cerebellum; relative size of facial lobes.

53. *Relative size of the cerebellum* – Positive correlations: *number of barbels; *relative size of vagal lobes; *relative size of facial lobes. Negative correlations: pelvic fin shape; relative eye size; fine structure of gill rakers; relative size of optic lobes.

54. *Relative size of the vagal lobes* – Positive correlations: *relative size of cerebellum. No significant negative correlations.

55. *Relative size of the facial lobes* – Positive correlations: position of pelvic fin; number of pelvic fin rays; *position of the mouth; relative size of cerebellum. Negative correlations: pelvic fin shape; aspect ratio of pelvic fin; fine structure of gill rakers; relative size of optic lobes.

56. *Relative size of the acoustic tubercles* – No significant correlations.

Factor Analysis.—Factor analysis of morphological characters was useful in pointing out some relationships not seen in the linear correlation analyses. Moreover, its basic property of ordering the importance of the covarying characters resulted in a ranking of trends which would not otherwise have been possible. The first three factors identify the three primary trends in the ecological differentiation among the fishes studied. These factors combine variables which relate to, respectively, technique of predation, maneuverability and utilization of habitats, and vertical zonation. These trends and all other trends defined by the factor analysis together with the associated resultant separations of species are described below. Altogether, the factor analysis indicated nine significant multivariate trends in the covariation of characters which jointly accounted for 79% of the total variance.

Factor 1, the major trend accounting for 31% of the character variance, indicated an association of several characters which relate to feeding behavior and technique. It indicates a positive association among having a high number of branchiostegal rays and the presence of jaw teeth (especially canines) and having many small teeth on the gill rakers; and a negative association of these characters with the presence of hypertrophied pharyngeal teeth and much red muscle in the peduncle. I interpret this to mean that the major morphological trend in ecological separation of the fishes studied has been in differentiation in feeding strategy between "lie-and-wait" biting predators (high scores on factor 1) and cruising suction feeders (low scores on factor 1). The ordination of families which results from consideration of this factor goes from Esocidae (pikes) with high factor scores through Percidae (perches), Ictaluridae (catfishes), and Centrarchidae (sunfishes) to Cyprinidae (minnows) with low scores (Fig. 1).

Factor 2 (12% variance) indicated the association among a number of characters relating to habitat separation by differences in body shape and proportions (see section on interpretation of morphological characters below). This factor associated a high ratio of caudal span to body depth, a large number of pelvic fin rays, and the location of both pelvic and dorsal fins entirely posterior to the center of gravity of the fish with low values for both the flatness index and relative body depth, short paired fins, pelvic fins which are rounded and located near the center of gravity of the fish and small relative eye size. Thus this factor separated the pickerel-like morphology at one extreme and the sunfish-like morphology at the other. Figure 2 shows the factor scores for the species on this factor.

Factor 3 (10% variance) identified characters associated with a benthic habit. Thus it associated large pectoral fin area with a small swim bladder and dorsally displaced eye position. Darters, naturally, showed especially high scores on this character (Fig. 3) and all suckers except *Erimyzon oblongus* showed somewhat positive scores. All other fishes showing positive scores on this factor I also infer to have a benthic preference (Fig. 3).

Factor 4 (7% variance) indicated the next most important trend in character variation among the fishes studied was that of being a small insectivore (see below). The major association shown by this factor was between small size and having a short relative gut length. To a lesser extent, these morphological features were also associated with presence of hooked pharyngeal teeth, few gill rakers, a supraterminal or terminal mouth which opens anteriorly, a long relative peduncle length and a large relative eye size. Fishes with high scores included both mid-water minnows and darters, *Gambusia affinis* and *Aphredoderus sayanus*; whereas sunfishes, pickerels, catfishes, and especially suckers had low scores (Fig. 4).

Factor 5 (6% variance) and Factor 6 (4% variance) each indicated associations of characters which differentiate two families. Factor 5 identified the relationship between having barbels, having a flattened peduncle and having few pectoral fin rays. All these characters are specializations of catfishes (Fig. 5). Factor 6 identified the association of large mouth size with large head size and having rounded pectoral fins placed near the center of gravity of the fish. Thus it identified a suite

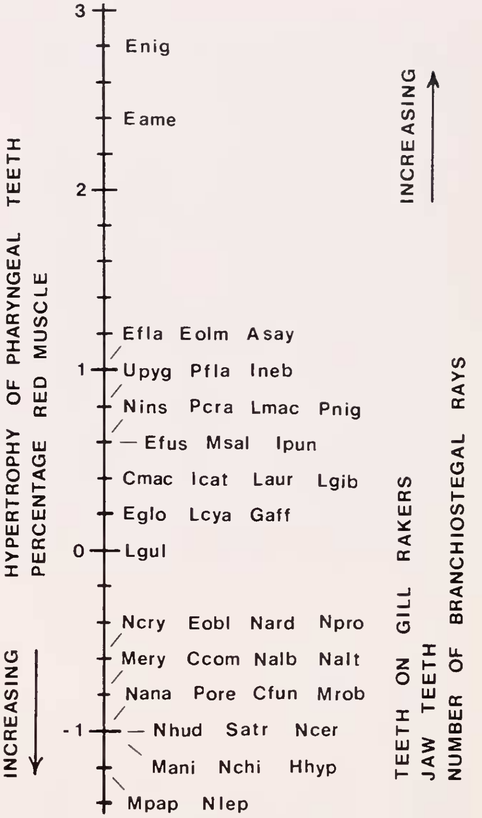

FIGURE 1. Ordination of species by mean factor scores on Factor 1 of the factor analysis of morphology. See text for interpretation. Abbreviations for species names are: Asay = *Aphredoderus sayanus*; Ccom = *Catostomus commersoni*; Cfun = *Clinostomus funduloides*; Cmac = *Centrarchus macropterus*; Eame = *Esox americanus*; Efla = *Etheostoma flabellare*; Efus = *Etheostoma fusiforme*; Eglo = *Enneacanthus gloriosus*; Enig = *Esox niger*; Eobl = *Erimyzon oblongus*; Eolm = *Etheostoma olmstedi*; Gaff = *Gambusia affinis*; Hhyp = *Hybopsis hypsinotus*; Icat = *Ictalurus catus*; Ineb = *Ictalurus nebulosus*; Ipun = *Ictalurus punctatus*; Laur = *Lepomis auritus*; Lcya = *Lepomis cyanellus*; Lgib = *Lepomis gibbosus*; Lgul = *Lepomis gulosus*; Lmac = *Lepomis macrochirus*; Mani = *Moxostoma anisurum*; Mery = *Moxostoma erythrurum*; Mpap = *Moxostoma pappillosum*; Mrob = *Moxostoma robustum*; Msal = *Micropterus salmoides*; Nalb = *Notropis alborus*; Nalt = *Notropis altipinnis*; Nana = *Notropis analostanus*; Nard = *Notropis ardens*; Ncer = *Notropis cerasinus*; Nchi = *Notropis chiliticus*; Ncry = *Notemigonus chrysoleucas*; Nhud = *Notropis hudsonius*; Nins = *Noturus insignis*; Nlep = *Nocomis leptocephalus*; Npro = *Notropis procne*; Pcra = *Percina crassa*; Pfla = *Perca flavescens*; Pnig = *Pomoxis nigromaculatus*; Pore = *Phoxinus oreas*; Satr = *Semotilus atromaculatus*; and Upyg = *Umbra pygmaea*.

of characters which indicate ecological specializations shared by most sunfishes and which differentiate them from the other fishes (Fig. 6).

The remaining three factors, together accounting for only 9% of the variance, did not in fact demonstrate clear cut morphological patterns. Factor 7 identified species which lack a lateral line canal (Fig. 7). Perhaps the most important point here is that although this character was assumed to indicate benthic habitat preferences (see below), the factor analysis did not associate it with the other characters in Factor 3. Factor 8 did not show any easily interpretable result but identified a weak association between small pelvic fin size and a low number of caudal fin rays (Fig. 8). Factor 9 identified species with extremely long, thin gill rakers (Fig. 9). There was also a tendency for a high index of trunk shape to be associated with this factor.

Gut Content Analysis. The results of the gut content analyses for the 33 common species are presented in Table 1 according to the coded format described previously. Notably, no two species were found to have the same diet in both size and composition. This result was obtained even with the relatively small sample size of individuals per species compared to most fish studies (e.g., Keast, 1966; Nilsson, 1960; Schwartz and Dutcher, 1962; although see also Carpenter, 1940) and the gross nature of the food categories. Dietetically, perhaps the two most similar

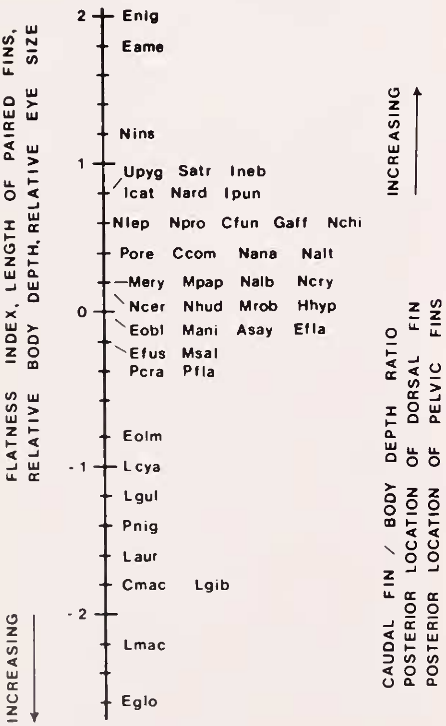

FIGURE 2. Ordination of species by mean factor scores on Factor 2 of the factor analysis of morphology. See text for interpretation. Abbreviations as in legend for Fig. 1.

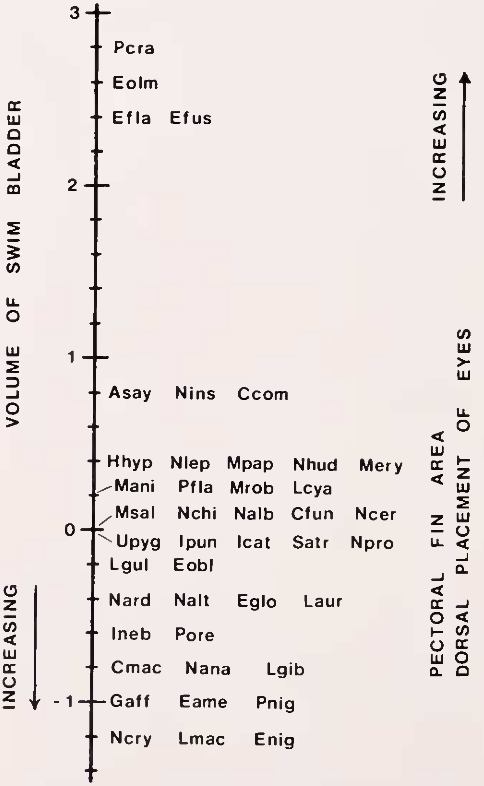

FIGURE 3. Ordination of species by mean factor scores on Factor 3 of the factor analysis of morphology. See text for interpretation. Abbreviations as in legend for Fig. 1.

sympatric species were *Clinostomus funduloides* and *Semotilus atromaculatus*. Both of these species fed exclusively on terrestrial insects, but *Semotilus* took larger prey items in both relative and absolute terms. *Gambusia affinis* and *Notropis ardens* similarly differ only in prey size in this study, but were not found in the same stream.

A factor analysis with orthogonal rotation was performed on the food data in an effort to define trends in types of prey eaten. Nine factors accounting for 80% of the total variance were identified. The major trend (Factor 1 – 23% total variance) was one of prey size. Factor 1 separated predators on small items from those on large items, especially fish. Factor 2 (18% total variance) identified the second most important trend in feeding to be one relating to vertical position of prey. It separated bottom feeding as defined by the presence of ostracods, molluscs, filamentous algae and silt in the gut from surface feeding as defined primarily by eating terrestrial insects. All remaining factors merely identified individual food categories in order of their relative importance to numbers of species of fishes. Factor 3 (13% variance) identified the insects as the most important prey type and also indicated the tendency of fishes to eat either aquatic insects or terrestrial ones, but not both. Factor 4 (10% variance) related to

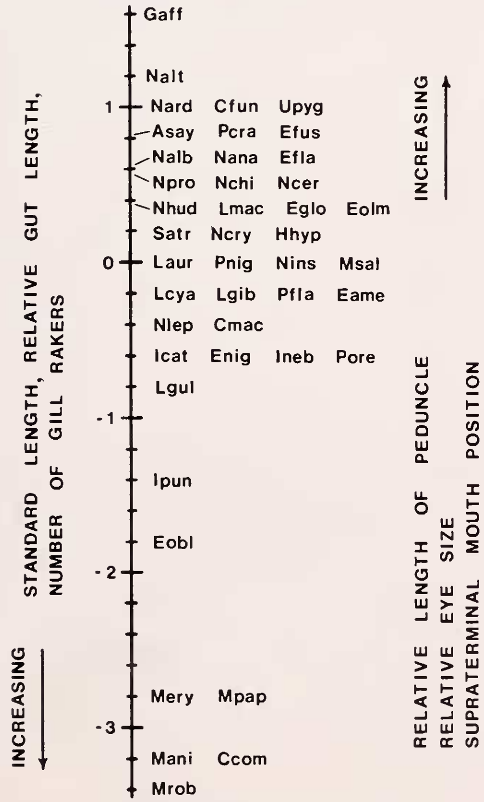

FIGURE 4. Ordination of species by mean factor scores on Factor 4 of the factor analysis of morphology. See text for interpretation. Abbreviations as in legend for Fig. 1.

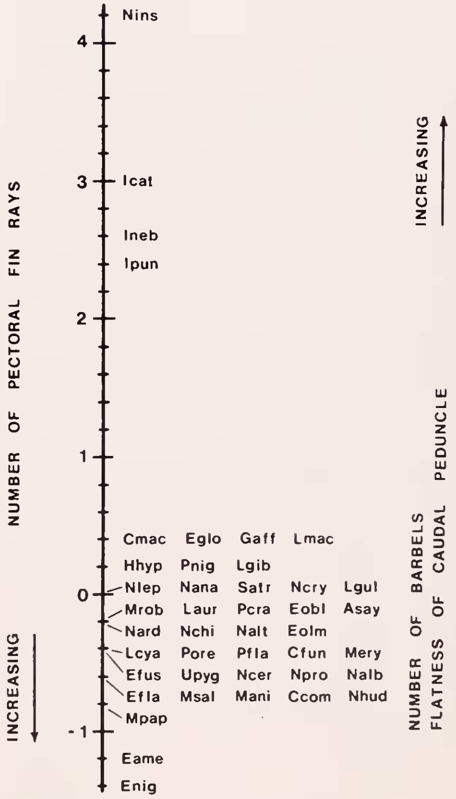

FIGURE 5. Ordination of species by mean factor scores on Factor 5 of the factor analysis of morphology. See text for interpretation. Abbreviations as in legend for Fig. 1.

ship, could be demonstrated. Exceptions to this generalization are noted below where the characters are discussed seriatim. For each character the significance assumed at the outset, support from the literature, and the results of this study are given.

Superficial body and body shape characters

1. Standard length was assumed to be an indicator of prey size. Numerous studies of fish usually involving only a single species (e.g., Swynnerton and Worthington, 1940; Lindstrom, 1955 and references cited therein; Nilsson, 1955, 1958; Thomas, 1962; Hall *et al.*, 1970) have shown prey size to increase as a function of increase in body size. I found absolute prey size to be positively correlated ($r = 0.690$, $P < 0.001$) with standard length as was predicted. Relative prey size was not so correlated ($r = 0.309$, $0.10 > P > 0.05$). The correlation demonstrated here for this widely assumed relationship in ecological work (see Schoener and Gorman, 1968; Ashmole, 1968; Pianka, 1969; among others) is unusual in having been established for so broad a range of taxa.

2. Pigmentation pattern was assumed to indicate habitat and behavior according to the scheme of Nikolskii (1963). Nikolskii indicated the following correlates: (1)

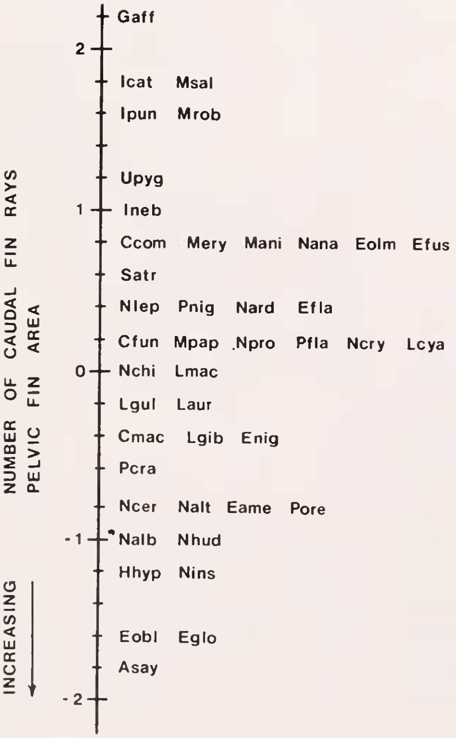

FIGURE 8. Ordination of species by mean factor scores on Factor 8 of the factor analysis of morphology. See text for interpretation. Abbreviations as in legend for Fig. 1.

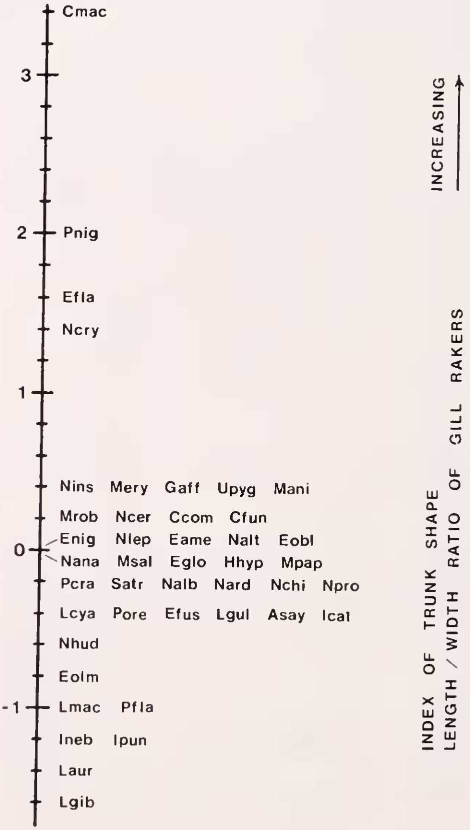

FIGURE 9. Ordination of species by mean factor scores on Factor 9 of the factor analysis of morphology. See text for interpretation. Abbreviations as in legend for Fig. 1.

eating copepods; Factor 5 (8%), diatoms; Factor 6 (6%), terrestrial invertebrates; Factor 7(5%), amphipods and isopods; Factor 8 (4%), filamentous algae; and Factor 9 (3%), crayfish.

The results of the gut content analyses for the rare species according to decreasing order of importance of categories present are: *Anguilla rostrata* – empty; *Umbra pygmaea* – aquatic insects; *Notropis hudsonius* – aquatic insects, silt; *Moxostoma anisurum* – aquatic insects, molluscs, ostracods, copepods, and silt; *M. erythrurum* – aquatic insects, ostracods, diatoms, silt and sand; *M. pappillosum* – ostracods, vascular plants, silt; *M. robustum* – aquatic insects, sand; *Ictalurus catus* – terrestrial insects, sand (gut nearly empty); *I. punctatus* – crayfish, aquatic insects, terrestrial insects, vascular plants; *Enneacanthus gloriosus* – aquatic insects, terrestrial insects; and *Percina crassa* – aquatic insects and sand.

These results were utilized below in the interpretation of the morphological characters.

Interpretation of Morphological Characters.—The initial choice of all characters was based on some inferred functional and/or ecological significance. Although in most cases there was some precedent in the literature for the supposed association between character and function, the experimental substantiation of any particular association has been extremely rare. In fact, seldom have data been compiled (but see Aleev, 1969) so that even a statistical correlation, let alone a causal relation-

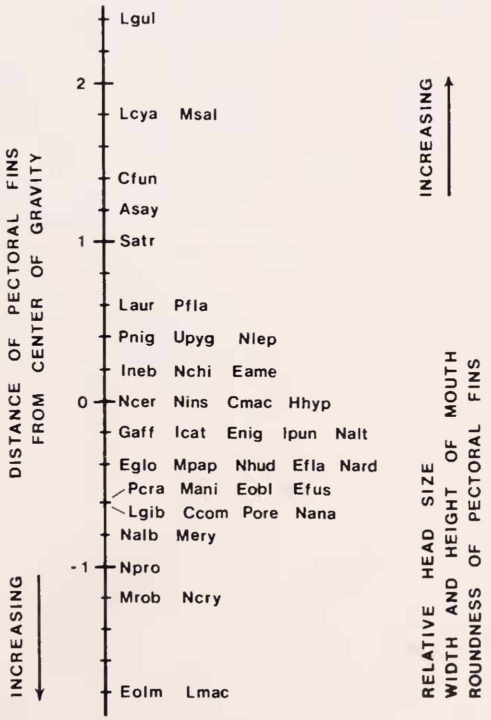

FIGURE 6. Ordination of species by mean factor scores on Factor 6 of the factor analysis of morphology. See text for interpretation. Abbreviations as in legend for Fig. 1.

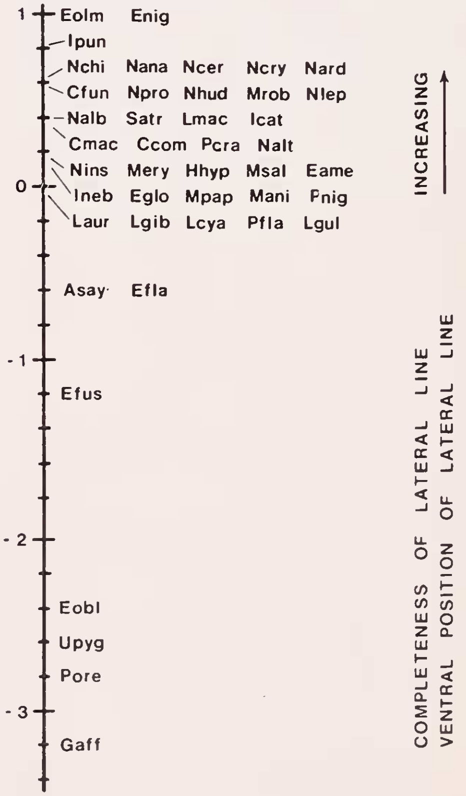

FIGURE 7. Ordination of species by mean factor scores on Factor 7 of the factor analysis of morphology. See text for interpretation. Abbreviations as in legend for Fig. 1.

silvery or reflective sides – solitary pelagic; (2) countershading with a dark lateral band – schooling pelagic; (3) mottled pattern or vertical bars – vegetal or benthic rocks; and (4) countershading without either silveriness or a lateral band – benthic over a sand bottom.

3. Completeness of the lateral line canal was assumed to be an indicator of habitat and behavior also. This sensory structure which detects water movements tends to be best developed in active fishes and reduced or absent in bottom dwellers and sluggish forms (Branson and Moore, 1962).

4. The position of the lateral line canal was assumed to relate to vertical habitat position and to the predation relations of the fish. The character states used and the particular associations were: (0) lacking – benthic or sluggish forms; (1) curving dorsally – fishes which have predators and/or prey dorsal to them in the water column; (2) horizontal – predators in the upper and midwater region; and (3) curving ventrally – fishes which feed high in the water column and are subject to predation from below (Marshall, 1971; Disler, 1971).

5. Relative head length was assumed to be related to prey size, a fish with a relatively larger head being able to handle relatively larger prey. To the best of my knowledge this relationship has not previously been studied in fishes, although Schoener (1968) has demonstrated it to hold for certain lizards. My results show that both absolute ($r = 0.697$, $P < 0.001$) and relative ($r = 0.701$, $P < 0.001$) prey size are positively correlated with relative head length. Thus, large headed little fish like *Aphredoderus sayanus* took large prey. Both relative head length and standard length are shown in this study to be equally good predictors of absolute prey size, but only the former seems strongly related to relative prey size.

6. Flatness index was assumed to indicate habitat water velocity with a lower index being associated with more rapidly flowing water (H.E. Evans, 1950; Hora, 1922; Nikolskii, 1933). As noted above, this character and the next showed a significant positive correlation with each other as well as being associated in the factor analysis (Factor 2, Fig. 2). Both of these results should be expected given the predicted common dependence of these characters on habitat water velocity.

7. Relative body depth was assumed to be inversely related to habitat water velocity and directly related to capacity for making vertical turns, i.e., about the axis of pitch (Nikolskii, 1933; Aleev, 1969). Significant differences in relative body depth were found between samples of each of three species of centrarchids collected in two different streams (Table 2). For two of the species, an increased sample size was employed to guard against the possibility of a non-random error in the initial measurement or sampling which involved only ten individuals.

The intraspecific differences would support the proposed interpretation if (1) habitat water velocity were higher in East Prong Little Yadkin (Pee Dee) than in Maho Creek (Roanoke) and higher in the latter than in Mud Creek (Cape Fear); and (2) the morphological variation were due to adaptation to these local physical conditions. The required differences in habitat water velocities seem likely. East Prong Little Yadkin has a gradient three to four times greater than the other two streams and hence would be expected to have a mean velocity one and a half to two times greater than either of the others (Hynes, 1970). The few pools which are present are small and isolated backwaters are virtually nonexistent. Thus likely both *Lepomis auritus* and *Lepomis cyanellus* are subjected to a stronger selective pressure for increased tolerance to flowing water in East Prong Little Yadkin than in Maho Creek. Alternative possibilities, e.g., character displacement, or in the case of the introduced *L. cyanellus*, founder effect, do exist, but seem less likely. With regard to the comparison of *Pomoxis nigromaculatus* in the two streams, a higher mean velocity is expected in Maho Creek than in Mud Creek because although the

TABLE 1. Results of the gut content analyses for the 33 common species of fishes. The numerical entries in the table for each food category are character codes for, respectively, frequency and importance of that particular prey type in the diet of the species. For a complete explanation of the coding , see the methods section of the text.

	Fish	Copepods	Ostracods	Aquatic insects	Terrestrial insects	Crayfish	Amphipods and isopods	Diatoms	Filamentous algae	Molluscs	Sand	Silt	Terrestrial inverts	Vascular plants	Absolute prey size	Relative prey size
Esox americanus	23	11	11	23	22	55	1	11	11	1	1	1	22	1	4	4
Esox niger	55	22	11	33	11	33	1	11	11	1	1	1	22	1	6	5
Clinostomus funduloides	11	11	11	11	66	11	1	11	11	1	1	1	11	1	2	2
Hybopsis hypsinotus	11	23	11	55	23	22	1	22	11	1	1	5	11	1	1	2
Nocomis leptocephalus	11	11	11	45	23	23	1	23	11	1	4	1	11	1	2	2
Notemigonus crysoleucas	11	22	11	33	34	11	1	44	23	1	2	4	11	1	1	1
Notropis alborus	11	11	11	33	23	11	1	34	11	1	1	3	11	1	1	1
Notropis altipinnis	11	11	11	11	55	11	1	11	33	1	1	1	11	1	1	2
Notropis analostanus	11	11	11	33	55	11	1	22	23	1	1	2	11	1	1	2
Notropis ardens	11	11	11	33	55	11	1	11	11	1	1	1	11	1	2	2
Notropis cerasinus	11	11	11	65	43	11	1	11	22	1	1	3	11	1	3	3
Notropis chiliticus	11	11	11	33	45	11	1	11	33	1	2	1	11	1	2	2
Notropis procne	11	11	11	44	22	11	1	44	22	1	1	4	11	1	1	1
Phoxinus oreas	11	11	11	23	11	11	1	65	11	1	1	6	11	1	1	1
Semotilus atromaculatus	11	11	11	11	66	11	1	11	11	1	1	1	11	1	3	4
Catostomus commersoni	22	11	32	65	23	32	1	11	33	1	6	3	23	1	3	2
Erimyzon oblongus	11	44	33	43	11	11	1	23	32	1	2	6	22	1	1	1
Ictalurus nebulosus	11	11	44	33	11	22	1	11	33	2	3	5	11	2	2	1
Noturus insignis	11	11	11	65	22	11	1	11	11	1	6	1	11	1	2	1
Aphredoderus sayanus	11	11	11	55	11	11	2	11	11	1	2	2	23	1	3	6
Gambusia affinis	11	11	11	33	55	11	1	11	11	1	1	1	11	1	1	1
Centrarchus macropterus	23	23	11	43	44	11	1	11	11	1	1	1	11	1	3	3
Lepomis auritus	11	11	11	54	33	33	1	11	11	1	1	1	23	2	4	4
Lepomis cyanellus	11	11	11	43	33	44	2	11	11	1	1	2	11	1	4	5
Lepomis gibbosus	11	11	33	56	43	11	1	11	22	1	1	4	11	1	2	2
Lepomis gulosus	11	11	11	44	43	33	1	11	11	1	1	1	11	1	4	5
Lepomis macrochirus	11	22	11	55	43	11	1	11	11	1	1	2	11	1	2	2
Micropterus salmoides	33	11	11	23	44	23	1	11	11	1	1	1	11	1	3	4
Pomoxis nigromaculatus	33	22	11	11	65	33	1	11	11	1	1	1	22	1	3	2
Etheostoma flabellare	11	11	11	65	11	11	1	11	11	1	1	1	22	1	2	3
Etheostoma fusiforme	11	43	11	65	11	11	1	11	11	1	1	1	11	1	1	2
Etheostoma olmstedi	11	11	11	65	11	11	1	11	11	1	3	1	11	1	1	2
Perca flavescens	11	11	11	65	11	33	1	11	11	1	1	1	11	1	2	2

TABLE 2. Intraspecific variation in relative body depth (see text for definition) in three species of centrarchids. NM= not measured.

Species	n	East Prong	Mud Cr.	Maho Cr.	F value	Signif.
Lepomis auritus	15	0.397	NM	0.444	9.806	< 0.01
Lepomis cyanellus	10	0.379	NM	0.395	5.804	< 0.05
Pomoxis nigromaculatus	28	NM	0.431	0.403	8.874	< 0.01

gradients are similar in both, the former is larger (Hynes, 1970). Again, the observed differences correspond to the hypothesized interpretation of the character. No other species was found to show intraspecific variation in this character. Such variation has been reported in Gromov (1973) who compared lake and river populations of carp.

8. Index of trunk shape was assumed to be directly related to hydrodynamic ability in that a high value is associated with a late separation of the boundary layer (Aleev, 1969; Ovchinnikov, 1971). Hence higher values are assumed to indicate fishes which spend more time cruising. However, Aleev (1969, Table 21) did point out that body height affects the index so that deep bodied fishes are apt to have higher values than one might expect from their swimming habits.

My results tend to substantiate Aleev's findings. In the first place, I did not find this character to show a significant correlation with any other. Inasmuch as other characters were also assumed to relate to various aspects of hydrodynamics and cruising, this suggests either that this character measures some unique aspect of swimming ability, or that there are other irregularities in the values. The ordination of species means for this character suggests the latter to be the case as high values are recorded both for cruising minnows and for several species of laterally flattened, deep bodied centrarchids. Thus my results indicate the same ambiguity in the significance of this index as those of Aleev (1969).

9. Relative peduncle length was assumed to be directly related to swimming ability (Hora, 1922; Kanep, 1971).

10. Caudal peduncle flatness index was assumed to relate inversely to amplitude of swimming movements (Nursall, 1958) and, like flatness index of the body, to be higher in less active swimmers. In general, a listing of species according to increasing value for this character produced an ordination of species which, based on literature description of their habits, would be concordant with the assumed significance. Thus, for example, *Pomoxis nigromaculatus* showed a higher index than *Lepomis auritus* and *L. cyanellus* which in turn showed higher values than *Micropterus salmoides*.

Caudal fin characters

11. Aspect ratio of the caudal fin was assumed to be directly proportional to the amount of swimming the fish does (Nichols, 1915; Harris, 1953; Nursall, 1958; Aleev, 1969; Kramer, 1960). The positive correlation of this character with the percentage of red muscle in the peduncle is the most tangible evidence for the assumed function (see discussion of red muscle, below).

12. Caudal span/body depth ratio was assumed to be directly proportional to speed of swimming in that ratios of increasing magnitude greater than one indicate better hydrodynamics for the caudal fin as the lobes of the fin are out of the zone of vortices shed from the body (Aleev, 1969). I found low values for sunfishes and high values for minnows which, according to the hydrodynamic argument

presented above, would imply that minnows are faster swimmers than sunfishes. Experimental substantiation of this is lacking.

13. The number of caudal fin rays was assumed to be directly proportional to the significance of the caudal fin as the principal means of locomotion (Marshall, 1971). My results suggest the separations of species given by this character may well be more phylogenetic than functional or ecological for my species. For instance, all sunfishes had 17 caudal fin rays, suckers had 18, and both minnows and pickerels had 19.

Paired fin characters

Although the importance of the paired fins in low speed maneuvering has been investigated by a number of persons (e.g., Aleev, 1969; Breder, 1926; Gosline, 1971; Gray, 1968; Harris, 1953), precise associations between functional specializations and particular morphological features have not always been defined. Thus for some of the following characters, no definite functional correlate is given but rather an assumed function based on theoretical considerations.

14. Pectoral fin length was assumed to increase as a function of amount of low speed maneuvering in the behavior of the fish (Gray, 1968; Starck and Schroeder, 1970; Kanep, 1971). Factor 2 of the factor analysis indicates an association between high values in this character and body shape characters which indicate low habitat water velocity (see Fig. 2). One might expect a fish in quiet water to do more low speed maneuvering than one living in fast water.

15. Aspect ratio of the pectoral fin was assumed likely to relate in some manner to the ways the fin might be able to function. The only correlation found for this character was with the next.

16. Relative pectoral fin area was assumed to be directly proportional to the capacity of the fin to function in braking, fanning to maintain position, and acceleration from the stop (Gosline, 1971). My results, particularly Factor 3 of the factor analysis (Fig. 3), indicate large relative pectoral fin area is also associated with benthic habits. Recently, A.N. Jones (1975) also reported pectoral fin area to relate to benthic living, particularly in areas of current. Jones found that salmon had larger pectoral fins than trout and were more frequently found in riffles. He suggested that the larger pectoral fin of the salmon enables it to "hold station" in riffles by deflecting water over the fin and thereby enable salmon to occupy territories unavailable to trout. Keenleyside (1962) reported observations made while skin diving which confirm this interpretation. He observed that salmon rest on the bottom with their pectoral fins spread, whereas trout do not maintain contact with the bottom, but rather usually swim actively against the current to maintain position. For additional information, see also Lundberg and Marsh (1976) who discuss how suckers use their pectoral fins on the substrate.

17. Relative distance of the pectoral fin from the center of gravity of the fish was assumed to be directly proportional to the importance of the pectoral fin in the turning and maneuverability of the fish (Aleev, 1969; Breder, 1926) in that all else being equal, a larger distance from the center of gravity provides greater torque. The various correlations reported above for this character do not provide any real support for this argument.

18. Pectoral fin shape, like its aspect ratio, was assumed to relate to its function. One correlate in the literature is that rounded fins are characteristic of fishes which remain motionless in midwater (Aleev, 1969).

19. Position of the pectoral fin relative to the center of gravity was assumed to have something to do with the turning capacity of the fish.

20. Number of pectoral fin rays has been suggested by Hubbs (1941) to be directly proportional to the amount of time the fish spends in the current.

21. Pelvic fin length was assumed to be related to habitat preference, being longer

in rocky habitat species and shorter in free swimming species (Starck and Schroeder, 1970).

22. Aspect ratio of the pelvic fin was assumed to be small in fishes in which the pelvic fin is used only for a brake or forward swimming aid and large if the fins are important for backing and hovering (Harris, 1937).

23. Relative pelvic fin area was assumed to be largest in fishes with demersal habitat preference (Aleev, 1969).

24. Relative distance of the pelvic fin from the center of gravity of the fish was assumed to be an indication of torque and hence of the importance of the pelvic fin in the turning and maneuverability of the fish (Aleev, 1969; Breder, 1926).

25. Pelvic fin shape was assumed to relate to its function. One correlate in the literature is that more falcate pelvic fins are found in fishes which are constantly in the current (Hubbs, 1941).

26. Position of the pelvic fin relative to the center of gravity was assumed to lower with increased proportional use of the pectoral fin as brakes because the pelvics must be close to the center of gravity to counteract the pitch induced by such braking (Harris, 1938). Values were assumed to be higher with increased importance of the pelvic fins in turning movements (Breder, 1926).

27. Number of pelvic fin rays was assumed to be directly proportional to the amount of time the fish spends in the current (Hubbs, 1941).

28. Position of the dorsal fin relative to the center of gravity was assumed to reflect what functions the dorsal fin was capable of performing: (a) anterior rudder function is better the further anterior to the center of gravity the fin is, (b) keel function is best served at the level of the center of gravity, (c) stabilization of forward movement is associated with a posterior position, and (d) posterior rudder and/or locomotory function are best performed the further posterior the fin is positioned (Gosline, 1971).

Head characters

29. Relative eye size was assumed to be directly proportional to the development of visual capabilities in the fish (Protasov, 1970) and hence this character was assumed directly proportional to the importance of sight in the feeding of the fish (H.E. Evans, 1950).

Not all species reputed to be visual predators, e.g., *Esox niger*, had large relative eye sizes. Part of the explanation for this might be the known negative allometry of eye size in fishes (Martin, 1949). A transformation based on regressions of absolute eye size on standard length and using the intercepts as a measure of relative eye size merely gave a second value nearly perfectly correlated ($r = 0.9985$) with the original character.

Somewhat more disconcerting than the partially counterintuitive sequencing of some species in values for relative eye size was the low correlation of this character with relative size of the optic lobes, which was also assumed to be directly proportional to the development of visual capabilities in the fish. The Pearson coefficient was 0.455 ($0.01 > P > 0.005$) and the Spearman, 0.476 ($P = 0.005$). Still, enough of a trend appeared to be evident between visual habits of well known species and the relative eye size values for me to consider the use of this character to be valid.

30. Position of the eyes was assumed to relate to vertical habitat preference. Lateral placement was assumed to indicate pelagic habit and increased displacement dorsally was associated with the assumption of a more sedentary mode of life (Aleev, 1969). My results provide support for this interpretation. Although no significant simple correlations with this character were identified, the factor analysis (Factor 3, Fig. 3) did indicate it to be associated with several other characters which also were assumed to reflect benthic habitat preference.

31. Eye pigmentation was assumed to reflect habitat and behavior. The assumed correlates were: no pigmentation – slow

moving and/or benthic fishes; horizontal line of pigmentation – cruising habit; vertical line through the eye – fast turning habit; and presence of both a horizontal and a vertical line through the eye – both specializations (Barlow, 1972).

32. Position of the mouth was assumed to indicate the location of the food eaten relative to the fish (Aleev, 1969; Al-Hussaini, 1949; Schmitz and Baker, 1969). Schutz and Northcote (1972) provided experimental support for this interpretation. They found that Dolly Varden (*Salvelinus malma*) which have subterminal mouths were more effective bottom feeders than cutthroat trout (*Salmo clarki clarki*) which have terminal mouths and vice versa when both species were tested in aquaria. This evidence, notably, is only for two closely related species. My results which support the assumed interpretation are discussed below in conjunction with orientation of the mouth.

33. Orientation of the mouth was also assumed to indicate from where in the habitat a fish obtained its foods. Given that certain types of prey are apt to be found on or near the bottom (e.g., ostracods, diatoms, aquatic insect larvae) and others only at the surface or in mid-water (e.g., water striders, terrestrial insects, fishes), the existence of correlations between those types in the gut and mouth position and/or orientation can be determined. Due to the manner in which I coded position of the mouth and orientation of the mouth, one should expect positive correlations between these characters and items of benthic prey and negative correlations with surface and mid-water prey.

Table 3 shows the correlations for all prey categories with these two morphological features. The expected relations, although weak, do hold for ostracods, filamentous algae, aquatic insects and frequency of terrestrial insects. They were not demonstrated for diatoms or for fishes. The strongest positive correlations were with sand and silt, and the strongest negative, with prey size. The former cor-

TABLE 3. Correlations of gut contents with position and orientation of the mouth. The first figures for each category present coefficient and significance for frequency. The second figures give coefficient and significance for importance, where applicable (see text).

Gut content category	Correlations with position of the mouth		Correlations with orientation of the mouth	
Fish	-.31, NS	-.35, P <.05	-.24, NS	-.28, NS
Copepods	+.18, NS	+.17, NS	+.06, NS	+.02, NS
Ostracods	+.39, P <.05	+.31, NS	+.46, P <.01	+.38, P <.05
Aquatic insects	+.39, P <.05	+.40, P <.02	+.45, P <.01	+.47, P <.01
Terrestrial insects	-.43, P <.02	-.29, NS	-.44, P <.01	-.34, NS
Crayfish	-.29, NS	-.37, P <.05	-.15, NS	-.22, NS
Amphipods and isopods	-.28, NS		-.23, NS	
Diatoms	+.28, NS	+.34, NS	+.25, NS	+.30, NS
Filamentous algae	+.45, P <.01	+.38, P <.05	+.46, P <.01	+.40, P <.05
Molluscs	+.12, NS		+.15, NS	
Sand	+.63, P <.001		+.54, P <.002	
Silt	+.47, P <.01		+.48, P <.005	
Terrestrial invertebrates	-.12, NS	-.07, NS	-.14, NS	-.06, NS
Vascular plants	-.05, NS		-.01, NS	
Absolute prey size	-.55, P <.001		-.41, P <.02	
Relative prey size	-.60, P <.001		-.52, P <.002	

relations are considered very strong evidence that fishes with more ventral mouths obtain their prey from the bottom and those with more terminal or anterior mouths do not. The negative prey size correlation also supports the assumed significance of these characters in that the smallest prey items in this study, diatoms, tend to be benthic organisms in lotic habitats. Thus, my results indicate support for the hypothesized significances for both of these characters for a wide range of taxa.

34. Relative width of the mouth was assumed to be directly proportional to the size of food eaten (Aleev, 1969; Forbes and Richardson, 1920; Starck and Schroeder, 1970). My results pertaining to this character are discussed below with those for the next character.

35. Relative height of the mouth was also assumed to indicate size of prey. This is another of the few characters I used for which direct experimental evidence exists (Werner, 1974). Werner showed that optimal prey size for *Lepomis cyanellus* and *L. macrochirus* was a function of mouth size. My results show that both width and height of the mouth are highly significantly correlated with both relative and absolute prey size (for both Spearman and Pearson coefficients, all r's are between 0.594 and 0.681; all P's are less than 0.001). Thus my correlative evidence supports my having assumed generality of the type results obtained by Werner (op. cit.). Additionally, my extensive multifamily correlations also indicate that the correlations of prey size with gape (of the mouth) found by Thomas (1962) for two salmonids and Northcote (1954) for two cottids were not unique to these two families.

36. The index of protrusion was assumed to be greatest in fishes with the smallest prey. This is based on the assumption that strength of bite is inversely related to the degree to which the premaxillary is protruded and that a stronger bite is required to capture a large item of prey than a small one (Al-Hussaini, 1949; Aleev, 1969; Gosline, 1973).

My results do not support these assumptions. This index did not correlate negatively with either relative or absolute prey size ($r = -0.14$) among all species of fishes as should have been predicted. Five of the eight species taking prey of the largest relative prey sizes (*Esox niger, E. americanus, Aphredoderus sayanus, Semotilus atromaculatus,* and *Micropterus salmoides*) did have mouths with an index of protrusion of one or nearly one (i.e., no or very little protrusibility); however, so did such fishes as all members of the genera *Etheostoma* (darters) and *Ictalurus* (catfishes) which take prey of very small relative size. The other three predators on large relative size prey (*Lepomis auritus, L. cyanellus*, and *L. gulosus*) all had mouths which showed high values for this index. This character therefore seems to be of limited usefulness in comparing fishes between different families.

37. Number of barbels was assumed to be directly proportional to the importance of non-optic senses in feeding (Gilbert and Bailey, 1972) and the benthic habit of the fish (Gosline, 1973; Aleev, 1969). The barbels are innervated by the facial nerve so that one should expect this character to be strongly correlated with the relative size of the facial lobes. In fact, only the Pearson correlation of these two variables was significant ($r = 0.790$, $P < 0.001$) and not the Spearman.

38-40. Number of branchiostegal rays, presence of jaw teeth, and shape of jaw teeth were all assumed to be inversely related to the importance of suction in the capture of prey (Gosline, 1973). In addition, shape of jaw teeth was assumed to indicate size of prey.

One would not expect suction to be important in the capture of large prey, i.e., such items as fish or crayfish. In view of this expectation, the positive correlations of absolute prey size with number of branchiostegal rays ($P < 0.001$), with presence of jaw teeth ($P < 0.002$) and with the shape of jaw teeth ($P < 0.002$) provide evidence in support of the function I assumed for these characters. Additionally, my results provide further support for this proposed functional significance in that all three characters showed positive correlations with both frequency and importance of fish and crayfish (P's < 0.05 to < 0.001).

41. Hypertrophy of teeth on the pharyngeal arches was assumed to relate to manner of feeding, especially to be directly related to the importance of suction in capture of prey (Gosline, 1973). My results support this hypothesis in that a negative correlation was found between absolute prey size and this character ($P < 0.02$).

42. Shape of pharyngeal teeth was assumed to relate to dominant food type in the diet (H.E. Evans, 1950; Al-Hussaini, 1949). I found a weak positive correlation ($P < 0.05$) of the character with the frequency of occurrence of both filamentous algae and ostracods in the diet (recall the coding for this character provided a high value for teeth with grinding surfaces). No further significant correlations were determined. Apparently many different fish species, each with its own type of dentition, are able to eat from the same broad prey categories used in this study.

43. Number of gill rakers was assumed to be inversely correlated with the presence of larger and more benthic prey in the diet (Kliewer, 1970; Himberg, 1970; Nilsson, 1958). My results did not support a generalization of this observation on salmonids; in fact, they show the reverse relationship. Absolute prey size and number of gill rakers gave a positive correlation ($r = 0.519$; $P < 0.002$). Several factors enter into this: (1) considering the many reduced plates in *Esox* each to represent a gill raker so that those predators on large prey have among the highest gill raker counts; (2) the generally high gill raker counts among sunfishes; and (3) the generally low gill raker counts among minnows. Thus a strong taxonomic component negates the general utility of this character along lines such as those demonstrated by Kliewer (1970) and Himberg (1970).

In this study I varied my interpretation of the number of gill rakers depending on the degree of taxonomic relatedness of the species being compared. For intrafamilial comparisons, I assumed that the usual functional interpretation is correct and that a low number of gill rakers was indicative of large benthic prey. For general interfamilial comparisons, I interpreted differences in number of gill rakers by bearing in mind that the two strongest positive correlations with this character for all species are with items of the two largest prey size categories in the diet: (1) fish ($P < 0.001$) and (2) crayfish ($P < 0.01$). <

44. Shape of the middle gill raker, as measured by the ratio of length to width, was assumed to be inversely related to food size (Kliewer, 1970; Starck and Schroeder, 1970; Forbes and Richardson, 1920). My results lend little support to this assumption. No correlation between this variable and food size was found. Nor was this character correlated with any of the other morphological characters. The only correlation found was a weak positive association between shape of gill rakers (high values indicate long, thin gill rakers) and importance of copepods in the diet ($r = 0.373$, $P < 0.05$). This gives minor support to the functional interpretation assumed in this study, but obviously more parameters are operational in the selective regime for this feature than just the ability to obtain small mobile prey like copepods.

45. Finer structure of the gill rakers was assumed to relate to food type and food handling. My results supported this assumption as a number of significant relationships between prey and gill raker armament were observed. The strongest of these correlations are with prey size. High numbers of fine teeth on the gill rakers are correlated both with absolute size of prey ($r = 0.577$; $P < 0.001$) and relative size of prey ($r = 0.613$; $P < 0.001$). Weaker correlations were observed with individual categories of large prey types: crayfish ($r = 0.51$; $P < 0.002$); fish ($r = 0.42$; $P <$

0.02); and non-insect terrestrial invertebrates ($r = 0.39$; $P < 0.05$). Weak negative correlations were found with both diatoms ($r = -0.42$; $P < 0.02$) and filamentous algae ($r = -0.41$; $P < 0.05$), which indicated a tendency for fishes eating these latter two types of prey to have smooth or ridged gill rakers.

Internal body characters

46. Relative volume of the swim bladder was assumed to be inversely proportional to the bottom dwelling preference of the fish (Forbes, 1880; Bridge and Haddon, 1889) and also negatively correlated with water speed in the habitat of the fish (Hora, 1922; Gee, 1968, 1974). This latter relationship is one of the very few in which experimental evidence exists that demonstrates a causal relationship between ecological conditions and morphology. Gee (1970, 1972) and Gee et al. (1974) have presented data that indicate a number of species of fishes respond to an increase in water velocity in the laboratory by decreasing the volume of their swim bladders.

A complete listing of relative volume of the swim bladder (first value) and relative length of the swim bladder (second value) follows. Species are listed in order of increasing swim bladder volume and parentheses around a species name and values indicates that the sample size was 1 or 2 rather than the usual 10. The species mean values are: *Etheostoma flabellare* 0,0; *E. fusiforme* 0,0; *E. olmstedi* 0,0; (*Percina crassa* 0,0); *Aphredoderus sayanus* 0.036,0.282; (*Anguilla rostrata* 0.037, 0.200); (*Umbra pygmaea* 0.38,0.359); *Noturus insignis* 0.046,0.098; *Notropis chiliticus* 0.054,0.318; (*Notropis hudsonius* 0.054,0.341); (*Moxostoma robustum* 0.054,0.462); (*Ictalurus punctatus* 0.054, 0.182); *Nocomis leptocephalus* 0.056, 0.304; *Notropis ardens* 0.056,0.311; *Catostomus commersoni* 0.057,0.360; *Clinostomus funduloides* 0.061,0.340; *Perca flavescens* 0.061,0.330; *Erimyzon oblongus* 0.061,0.358; *Lepomis cyanellus* 0.061, 0.297; *Notropis procne* 0.062,0.321; *Semotilus atromaculatus* 0.063,0.344; *Notropis cerasinus* 0.064,0.363; (*Ictalurus catus* 0.065,0.186); *Ictalurus nebulosus* 0.066,0.197; *Esox niger* 0.067,0.415; *Micropterus salmoides* 0.068,0.314; *Phoxinus oreas* 0.068,0.336; *Hybopsis hypsinotus* 0.068,0.343; *Notropis analostanus* 0.069, 0.356; (*Enneacanthus gloriosus* 0.071, 0.343); *Lepomis gibbosus* 0.071,0.336; *Lepomis auritus* 0.072,0.315; *Gambusia affinis* 0.074,0.264; *Notropis altipinnis* 0.074,0.341; (*Moxostoma erythrurum* 0.075,0.473); *Moxostoma anisurum* 0.076,0.446; *Lepomis gulosus* 0.076, 0.341; *Notropis alborus* 0.078, 0.337; *Centrarchus macropterus* 0.079,0.426; *Lepomis macrochirus* 0.080,0.346; (*Moxostoma pappillosum* 0.083,0.465); *Esox americanus* 0.083,0.435; *Notemigonus crysoleucas* 0.083,0.378; *Pomoxis nigromaculatus* 0.085,0.364.

A comparison of habitat observations of the fishes with the values obtained in this study confirmed both of the points in the assumed significance of this variable. Known bottom dwellers in fast current regions had small swim bladder volumes. For example, all *Etheostoma* studied lacked gas-filled swim bladders and the bladder of *Noturus insignis* had a relative volume of only 4.6%. *Aphredoderus sayanus*, a bottom dwelling inhabitant of quiet water regions, also had a small swim bladder (3.6%). Pelagic, quiet water inhabitants, e.g., *Pomoxis nigromaculatus, Lepomis macrochirus,* and *Notemigonus crysoleucas* had large swim bladders (8.0-8.5%). Additionally, the factor analysis indicated relative volume of the swim bladder to covary with several other characters related with benthic habits (Factor 3, Fig. 3).

Comparisons of the actual magnitudes of the results listed above with a theoretical value which is assumed to give a fish neutral buoyancy are interesting. F.R.H. Jones (1951) calculated that if the average density of a fish were 1.076 g/cc, then a swim bladder volume equal to 7.06% of the total volume of the fish would be necessary to achieve hydrostatic equilibrium. Only a few species of fishes studied here showed mean values significantly different from this figure. *Notropis chiliticus, Noturus insignis, Umbra pygaea, Anguilla rostrata, Aphredoderus sayanus,* and all the darters had smaller percentage volumes and only *Pomoxis nigromaculatus* had a larger percentage volume than this theoretical figure. However, among the remaining species many significant differences did exist. These differences seem likely to reflect biological differences as stated above. Previously reported values of the percentage volume of the swim bladder in Cypriniformes have ranged from 5% to 10% (Alexander, 1959).

47. Relative length of the swim bladder was assumed to relate in the same way to the same qualities as relative volume of the same structure (Nelson, 1961; H.E. Evans, 1950). My results show that the ordination of species on this character would be similar to that obtained with the preceding (see listing above) and that the two characters are highly correlated (Pearson r = 0.88; $P < 0.001$). However, this character tends to have a stronger taxonomic component than the preceding. Thus even catfishes with fairly large relative swim bladder volumes (e.g., *Ictalurus punctatus*) have small relative swim bladder length. Suckers, especially those of the genus *Moxostoma* which have a three-part swim bladder, have large relative swim bladder lengths. Studies which encompass several families of teleosts and employ length of the swim bladder (or even length and depth but not width as Dobbin, 1941) as the sole estimator of buoyancy rest on shaky ground.

48. Relative gut length was assumed to be directly related to mud feeding, herbivory, and omnivory, and inversely related to carnivory and insectivory (H.E. Evans, 1950; Lagier et al., 1962; Forbes, 1888; Schmitz and Baker, 1969). My results support the "mud feeding" aspect especially, as positive correlations exist between this character and the presence of ostracods (P's < 0.02-0.002), diatoms (P's < 0.05-0.01), and silt ($P < 0.001$) in the gut.

49. Number of pyloric caeca was assumed to be correlated with the protein richness of the diet, as these structures function as an enzyme source and an area of absorption for protein nitrogen (Beamish, 1972; Phillips, 1969). My results show that the taxonomic component to this character was great. Thus, although some of the species for which I found piscivorous food habits (e.g., *Micropterus salmoides, Pomoxis nigromaculatus,* and *Centrarchus macropterus* – see Table 1) do have the most pyloric caeca, the most piscivorous of the fishes studied, *Esox niger*, lacks these structures.

50. Percentage of red muscle in the caudal peduncle was assumed to be directly proportional to the amount of sustained swimming or cruising that the fish does (Boddoke et al., 1959; Love, 1970; Gatz, 1973). Recently Roberts and Graham (1974) reported on the basis of electromyographic recordings that red muscle primarily is operating at slow swimming speeds in mackerel and that both red and white muscles increase in activity during acceleration.

The following listing of species by increasing percentage of red muscle corresponds generally to one's intuitive expectations given this function. Note sample size is 10 except for species in parentheses for which n = 1 or 2. Species mean percentages are: (*Umbra pygmaea* – 0%); *Etheostoma flabellare* – 0%; *E. fusiforme* – 0%; *E. olmstedi* – 0%; (*Percina crassa* – 0%); *Esox niger* – 1.8%; (*Enneacanthus gloriosus* – 2.2%); *Esox americanus* – 2.2%; *Aphredoderus sayanus* – 3.2%; *Pomoxis nigromaculatus* – 3.4%; *Lepomis cyanellus* – 3.9%; *Lepomis macrochirus* – 4.2%; *Lepomis gibbosus* – 4.2%; *Lepomis auritus* – 4.4%; *Micropterus salmoides* – 4.4%; *Gambusia affinis* – 4.5%; (*Anguilla rostrata* – 4.7%); *Erimyzon oblongus* – 4.7%; *Lepomis gulosus* – 4.7%; *Centrarchus macropterus* – 5.0%; (*Moxostoma anisurum* – 5.4%); *Perca flavescens* – 5.5%; *Notropis alborus* – 5.8%; *Phoxinus oreas* – 6.1%; *Ictalurus nebulosus* – 6.3%; (*Notropis hud-*

sonius – 6.6%); (*Moxostoma erythrurum* – 6.7%); *Hybopsis hypsinotus* – 6.7%; *Notemigonus crysoleucas* – 6.7%; (*Ictalurus catus* – 7.5%); *Notropis procne* – 7.5%; *Catostomus commersoni* – 7.7%; (*Moxostoma pappillosum* – 8.4%); *Noturus insignis* – 8.5%; *Notropis altipinnis* – 8.8%; *Semotilus atromaculatus* – 9.2%; *Notropis cerasinus* – 9.2%; *Nocomis leptocephalus* – 9.7%; *Clinostomus funduloides* – 9.8%; *Notropis analostanus* – 9.9%; *Notropis ardens* – 11.1%; (*Moxostoma robustum* – 11.3%); *Notropis chiliticus* – 12.0%; and (*Ictalurus punctatus* – 14.2%).

Most of the work in the literature in which actual measurements of stamina for swimming in fishes were made has been for salmonids (e.g., Brett, 1965, 1967, 1973; Hammond and Hickman, 1966; Hochachka, 1961; Horak, 1969, 1972; D.R. Jones, 1971; Stevens, 1968; and Vincent, 1960); none of these fishes occur in my study streams. A few papers do report on such non-salmonids as goldfish (Fry, 1958), smallmouth bass (Larimore and Duever, 1968), largemouth bass (Laurence, 1972) and bluegills (Oseid and Smith, 1972). However, only the work by Houde (1969) and Bainbridge (1960) was of an interspecific comparative nature such that one could compare the swimming abilities for two or more species with red muscle content. Houde (op. cit.) found little difference between two species of percids with the 9 to 15 mm total length larvae that he used. Gatz (1973) speculated on the possible relationship between differences in swimming performance among the three species tested by Bainbridge (1960) and differences in red muscle content and concluded the relationship assumed in this paper seemed operative.

Supportive evidence of a somewhat different sort comes from the work of Reddy and Pandian (1974) on the predation effectiveness of *Gambusia affinis* in flowing water. In addition to giving data which indicate a halving of predatory efficiency, they reported that the *Gambusia* appeared to have lost much energy in the flowing water and appeared to have very little available to spare for predation. Such results correspond nicely with the low amount (4.5%) of red muscle I found in this species and the proposed interpretation of this character. A similar experiment would be interesting with a species such as *Notropis chiliticus* or *N. ardens*, both of which have more than twice the red muscle *Gambusia affinis* has.

A further point of interest about the percentage of red muscle in the peduncle concerns the probable selective forces involved in achieving the observed values for this character. An ability to cruise slowly for prolonged periods with low metabolic expenditure readily enough would "explain" selection for red muscle. But why do some species lack it entirely (e.g., *Etheostoma*) or have very little (e.g., *Esox* and *Umbra*)? Two points come to mind. First, some fishes move about slowly, seemingly entirely by the movement of the paired fins. *Esox* and *Umbra* are examples, and the fin musculature of these species is red muscle. Second, if red muscle were metabolically more costly to maintain than white in a resting state, then one would expect its presence to be selected against in those species which do not demonstrate slow cruising behavior. Some evidence of just such a higher metabolic rate for red muscle for white has been given by Gordon (1968) and Lin et al. (1974).

Brain characters

51. Relative size of the forebrain was assumed to be directly proportional to the importance of olfaction in the life of the fish (Tuge et al., 1968) and also with nocturnal habits (H.M. Evans, 1940).

52. Relative size of the optic lobes was assumed to be proportional to the importance of vision in the species (Schwassman and Kruger, 1968).

53. Relative size of the cerebellum was assumed to be large in active, quick swimming fishes and in forms which live in fast water, but small in sluggish, slow water fishes (Herrick, 1924; Schnitzlein,

1964; Miller and Evans, 1965).

54. Relative size of the vagal lobes was assumed to be positively correlated with "mouth tasting," i.e., eating mud which is then sorted to a degree in the mouth using taste buds of the mucous membrane of the posterior oral cavity (Bhimachar, 1935; H.E. Evans, 1952; H.M. Evans, 1940).

55. Relative size of the facial lobes was assumed to be directly proportional to the importance of lip and barbel tasting in the feeding behavior of the fish (H.M. Evans, 1940; H.E. Evans, 1952; Miller and Evans, 1965).

56. Relative size of the acoustic tubercles was assumed to be directly proportional to the importance of the lateral line system in the behavior of the fish (H.M. Evans, 1940; Tuge et al., 1968).

For all six characters relating to the hypertrophy of various lobes of the brain, my results placed at least some species for which behavior was known at seemingly appropriate positions in the ordinations obtained. For example, *Anguilla rostrata* and members of the genus *Ictalurus* have large forebrains; and cyprinids have relatively larger cerebellums than centrarchids. The assumption that other less known species were in appropriate relative positions did not seem unwarranted. Few studies have been done comparing the relative importance of different senses in feeding and thus, by assumption in this study, with the relative sizes of different brain lobes. The only such paper of which I am aware which involved a species in this study was that by Roberts and Winn (1962). They found *Etheostoma olmstedi* (I changed the nomenclature here to correspond with Cole, 1967, 1972) to rely much more heavily on sight than olfaction. This corresponds well with my results. I found that *E. olmstedi* had one of the smallest values for relative size of the forebrain and one of the largest for relative size of the optic lobes of all those species measured.

Caveats and Summation

Bock and von Wahlert (1965) point out that any particular anatomical feature or structure may serve multiple functions and thus be subject to natural selection as a part of any of several form-function complexes. They suggested that the biological role of any feature cannot be deduced from the mere study of the form-function complex, but must be determined by direct observation of the organism. Alternatively, it would seem that if natural selection has operated in a repeatable manner to cause a regular association between a particular morphological feature and one form-function complex, then evidence for this should exist as a constancy of utilized faculties for the particular feature. Specifically, there should be strong correlations between such a feature and some manifestation of its biological role and also there should be correlations between this feature and others associated with the same role. For example, if a principal selective pressure on mouth size is always prey size, then there should be a correlation between prey size and any measure of mouth size among a group of species of fishes and correlations between the various measures of mouth size.

The results presented above attest to the validity of both points of view. First, the many significant correlations indicate that some repeatable selective forces do seem to be governing some portion of the variation in the morphological features measured. This should not be surprising in that each character was chosen on the basis that I felt the strongest single selective force operating on it was recognizable and in that these selective forces were at times the same for more than one character. In a number of cases, e.g., relative width and height of the mouth, strong correlative evidence in support of the hypothesized adaptation has been given. On the other hand, only about 2% of the between character correlations have coefficients of determination greater than 50%. This dearth of high correlations, especially between characters assumed to be responding to similar selective forces, gives support to the viewpoint of Bock and von Wahlert (1965). That is, the variability seen between features of presumed close functional relation could well be the result of selective pressures for two (or more) different faculties operating on the same feature. Complex rather than simple causative patterns for the correlations observed seem likely.

All of the support for any particular ecological interpretation of morphological features provided by this study is of a correlative nature. As Sokal and Rohlf (1969, Fig. 15.5) so effectively illustrate, a large number of causal patterns can result in correlations and these patterns need to be sorted out. Certain types of information would greatly aid in this area. First, experimental studies analogous to those of Gee et al. (1974), Machniak and Gee (1975), and Werner (1974) are necessary for many more features. Second, direct observations of fishes in their natural habitats of the sort made by Keeleyside (1962) would be especially useful for many of the habitat related characters. Hopefully the present work will be of heuristic value in indicating some of the features about which observations might be made most gainfully.

In answer to the questions posed originally, this study indicates that some significant portion of the biology of a freshwater stream fish is determinable from its morphology. While it is well known that fishes exhibit extreme plasticity of behavior when raised in monospecies cultures, they do tend to specialize in the presence of other species and interspecific competition (Nilsson, 1955, 1960, 1963, 1965, 1967; Ivlev, 1961; Trojnar and Behnke, 1974; Griffith, 1974; Andrusak and Northcote, 1971). Gorman and Karr (1978) report that for stream fish communities these specializations occur primarily in the selection of specific habitat types and secondarily in the preference for certain food resources if several are readily available within a given habitat. Earlier literature (Thomas, 1962; Gibbons and Gee, 1972; Keast and Webb, 1966; Lindsey, 1963; Schutz and Northcote, 1972) and the present study both indicate that many of these specializations are related to morphology. The functions and biological roles that are regularly associated with many morphological features are given above.

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